

TAXONOMY AND BIOGEOGRAPHY OF
PRIMULA SECT. *CUNEIFOLIA* (PRIMULACEAE)
IN NORTH AMERICA

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ABSTRACT

Section *Cuneifolia* is one of the smallest but most discrete sections in the large genus *Primula*. Its three members are characterized by cuneate leaves with dentate margins, globose capsules, and involute leaf veneration, and they are geographically distributed between the Sea of Okhotsk in Asia east to the Sierra Nevada of California. The three North American taxa are *P. cuneifolia* subsp. *cuneifolia*, *P. cuneifolia* subsp. *saxifragifolia*, and *P. suffrutescens*. *Primula cuneifolia* subsp. *saxifragifolia* is redefined here on the basis of its self-fertile homostylous flowers. It probably originated in the late Pleistocene at the edge of the Alaskan ice sheets when climatic perturbations disrupted the pollinator fauna. Section *Cuneifolia* is most closely allied to the widely disjunct sect. *Auricula* found in the mountains of central Europe. Although small, sect. *Cuneifolia* may have phylogenetic significance at the generic and family level due to its developmental patterns, biogeography, and reproductive biology.

Within the large genus *Primula* L. (Primulaceae, ca. 500 species), section *Cuneifolia* Balfour is one of the smallest and most biogeographically interesting groups. The three member species are distributed from northern Japan and northeastern Asia along the Sea of Okhotsk, through southern Alaska and the coastal mountains of Canada, and in the Sierra Nevada of California. The section is defined by cuneate leaf blades with dentate margins, conspicuous glandular development, globose capsules, and by the involute veneration of emergent leaves. The latter character is common in other genera in the Primulaceae, but is shared by only three of the thirty seven currently recognized sections in *Primula*, and considered primitive for the genus (Wendelbo 1961).

Two of the three species in sect. *Cuneifolia* are found in North America. *Primula suffrutescens* A. Gray is a rhizomatous species endemic to the Sierra Nevada in California. *Primula cuneifolia* Ledebour is found commonly in the Aleutian Islands, and more rarely throughout interior Alaska and the coast ranges south to British Columbia. It is also found in Asia as far south as northern Japan, along with the third member of the section, *P. nipponica* Yatabe, an alpine endemic on the island of Honshu.

Within the section, there has been taxonomic confusion only with the widespread species, *P. cuneifolia*. Four infraspecific taxa have

been previously described, based entirely on vegetative characters such as scape height, leaf length, and leaf dentation. In this paper I examine *P. cuneifolia* in North America and redefine two subspecies based on reproductive biology: *P. cuneifolia* subsp. *cuneifolia* which is distylous, and *P. cuneifolia* subsp. *saxifragifolia* which is homostylous.

Primula sect. *Cuneifolia* Balfour. J. Roy. Hort. Soc. 39:178. 1913.

Key to Members of Sect. *Cuneifolia* in North America

- a. Plants rhizomatous, leaves in clusters, often marcescent at stem base. *P. suffrutescens*
- a'. Plants not as above.
 - b. Flowers distylous. *P. cuneifolia* subsp. *cuneifolia*
 - b'. Flowers homostylous. *P. cuneifolia* subsp. *saxifragifolia*

Primula cuneifolia Ledebour, Mem. Acad. Imp. Soc. St. Petersburg 5: 522. 1815. See subspecies headings for synonymy and typification.

Plants efarinose with capitate glands on vegetative parts, glabrous. Stems herbaceous, not rhizomatous. Scape to 12 cm high, densely glandular. Leaves including petiole to 6 cm long, 0.8–1 cm wide, broadly cuneate, margins coarsely dentate, blade tapering to winged petioles. Involucral bracts lanceolate, plane at the base, densely glandular, to 0.5 cm long. Umbels 2–9 flowered; pedicels 0.3–2 cm long. Calyx green, 0.4–0.6 cm long, urceolate, divided up to $\frac{2}{3}$ the length by lanceolate teeth. Corolla deep pink to rose, rarely white, throat yellow; tube 0.5–1.2 cm long, slightly exerted from the calyx; 1.2–2.5 cm broad, deeply cleft. Stamens ca. 1.5 mm long. Stigma more or less capitate. Capsule globose at maturity, slightly shorter than the calyx. Seeds brown, 1–1.5 mm long, reticulate, angular with flanged edges.

Primula cuneifolia Ledebour subsp. *cuneifolia* (Fig. 1A)—TYPE: USSR. “in Sibiria transbaicalensis”. *Tilesius s.n.*? (holotype, LE?).

P. cuneifolia var. *Dubyi* Pax in Engler, Pflanzenreich, Primulaceae 112, 4:237. 1905.—TYPE: USSR. Siberia, Ajan. *Tiling 204* (holotype, LE?).

P. cuneifolia var. *elongata* Busch, Fl. Sib. & Orient. Extrem. 4:79. 1925.—TYPE: E. Busch, Fl. Sib. and Orient. Extrem. 4:78. Fig. B. 1925.

Scapes usually greater than 5 cm in height. Leaf petioles distinct, up to 4 cm long. Umbels with 3–9 distylous flowers. Anthers in pin flowers located near the middle of the corolla tube, stigma located just above the annulus; positions reciprocal in thrum flowers. Chro-

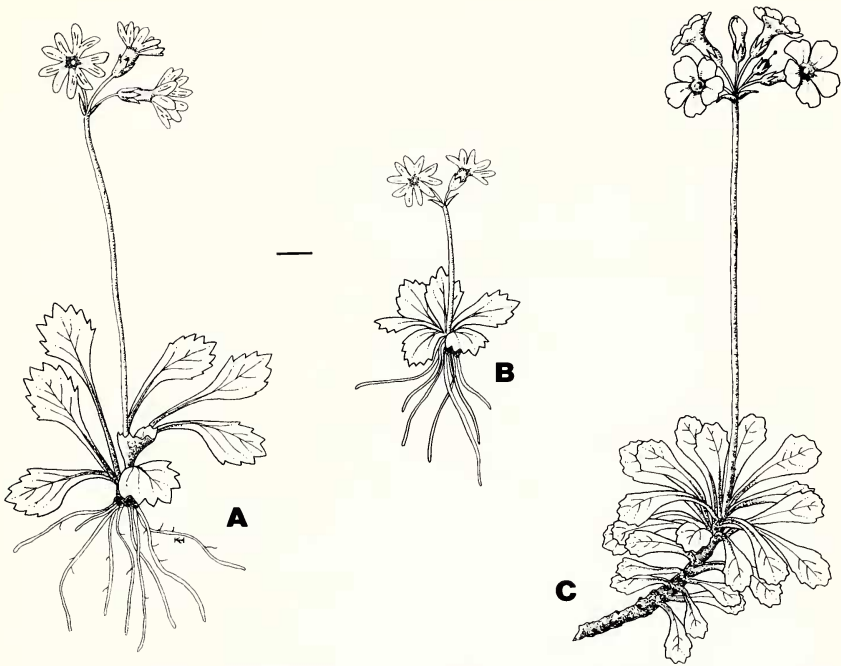


FIG. 1. A. *Primula cuneifolia* subsp. *cuneifolia*. B. *P. cuneifolia* subsp. *saxifragifolia*. C. *P. suffrutescens*. Bar indicates 1 cm.

mosome number: $2n = 22$ (Attu Island: Friedman 83-3 at ALA; Kamtschatka: Sokolovskaya 1968).

Distribution. Moist mixed herb meadows with acidic bedrock in Asia, along the Sea of Okhotsk from Hokkaido north to the Bering Strait; in North America known only from the Aleutian Islands of Attu, Agattu, and Adak (Fig. 2A).

Representative specimens. USA., Alaska, Aleutian Islands. Adak, O'Farrell 145 (ALA), Rausch 28 (CAS); Agattu, Trapp 23 (COLO); Attu, Brockner 5 (COLO), Chandler s.n. (GH), 28 Jun 1952, Coe s.n. (CAS), Friedman 83-3 (ALA), Hultén 6790 (CAS), Trapp 3 (ALA), Van Schaack 43-A (E), Williams 3113 (ALA).

***Primula cuneifolia* Ledebour subsp. *saxifragifolia* (Lehm.) Sm. & Forrest (Fig. 1B)**—*Primula* nov. sp. "saxifragaefol." (nomen nudum) Langsdorff, Reise um die Welt. 1812.—*Primula saxifragifolia* Lehmann, Monograph Primulaceae 89, t. 9. 1817.—*P. cuneifolia* var. *saxifragifolia* (Lehm.) Pax in Engler, Das Pflanzenreich, Primulaceae 112. 1905.—*P. cuneifolia* ssp. *saxifragifolia* (Lehm.) Sm. & Forrest, Notes Roy. Bot. Garden Edin-

burgh 16:20. 1928.—TYPE: USA. Alaska, Aleutian Islands, Unalaska, "Herb. Fischer" Unidentified collector, possibly *Langsdorff s.n. in 1805* (holotype, LE?, isotype, K!).

Scape less than 3.5 cm in height. Leaf petioles indistinct, up to 1 cm in length. Umbels with 1–4 homostylous flowers. Anthers and stigma located adjacent to one another near upper portion of corolla tube. Chromosome number: $2n = 22$ (*Kelso 85-20* at ALA).

Distribution. Moist alpine meadows and rocky slopes in Alaska throughout the Aleutian Islands and along the Bering Sea coast north to the Seward Peninsula, throughout the interior in alpine regions N to the Alaska Range, to the S in coastal mountains to northern Vancouver Island. Distribution in Asia unclear, but apparently common along the Bering Sea coast (Fig. 2A).

Representative specimens. USA, Alaska, Aleutian Islands, Adak, 20 Jun 1945, *Chandler s.n.* (CAS); Akuktan, *Macoun 94290* (GH); Amchitka, *Erdman 551* (COLO); Atka, *Eyerdam 1316* (K); Unalaska, *Friedman 81-37* (ALA); Unimak, *Eyerdam 1841* (CAS). Alaska Peninsula, Chignik, 19 Jul 1934, *Flock s.n.* (CAS); Cold Bay, 1924, *Cladden s.n.* (CAS); Port Moller, 11 Jul 1927, *Haley s.n.* (CAS); McNeil River, *Taggart 12* (CAS, COLO); Ugaiushuk Island, *Lawhead 137* (ALA). Alaska Range, Copper Mountain, *Mexia 2096A* (CAS); Denali National Park, *Teare 1636* (ALA); Kantishna Hills, *Kelso 85-20, 85-21, 85-22* (ALA); Lake Nerka, *Roberson 468* (ALA); Mt. Eielson, *Viereck 1165* (ALA, COLO, GH); Peters Hills Mts., *Siplivinsky 806* (ALA); Talkeetna Mts., *Helmstetter 110-79* (ALA). Alexander Archipelago, Juneau, *Anderson 6353* (GH), *Taylor 85* (ALA); Prince of Wales Island, *Vorobik 42* (ALA). Bering Sea, Golovin, *Rynning 1025* (ALA); Goodnews Bay, *Williams 3356* (ALA); Nunivak Island, *Utermohle 32* (ALA); St. Lawrence Island, 1928, *Haley s.n.* (CAS); St. Matthew Island, 8 Jul 1927, *Haley s.n.* (CAS). Chugach Mts., Hatcher Pass, *Harms 2925* (ALA); Seward, *Calder 5638* (GH); Thompson Pass, *Cooper 85-2* (ALA).

The Alaskan *Primula saxifragifolia* was made a subspecies of *P. cuneifolia* by Smith and Forrest (1928), based on their survey of the limited material then available from Alaska. The nature of the subspecies was extensively reviewed by Hultén (1937) who concluded that the Aleutian Island material described by Lehmann differed only in height, leaf size, and number of flowers. The homostylous flowers were first noticed by Smith and Fletcher (1948) but they were unable to survey enough material to detect if this character was diagnostic.

My examination of now ample material from Alaska indicates that *Primula cuneifolia* subsp. *saxifragifolia* is homostylous. This is the only feature that consistently distinguishes it from subsp. *cu-*

neifolia, although some vegetative characters can be useful as well. Subspecies *saxifragifolia* tends to be shorter than its Asiatic counterpart, and flowers often appear before the scape develops, although scape elongation continues during and after anthesis. It also tends to have shorter petioles and fewer flowers than subsp. *cuneifolia*. Because the morphological differences between the subspecies overlap and reproductive biology is the only feature that reliably distinguishes them, it seems appropriate to retain subspecific rank for these taxa.

Primula cuneifolia is represented in Japan by two additional taxa, subsp. *hakusanensis* (Franch.) Smith & Forrest, and subsp. *heterodonta* (Franch.) Smith & Forrest. The former is distinguished by its more shallow dentation of the leaf margins, and the latter by its irregular dentation. Both are distylous, and narrowly endemic to alpine areas on the northern island of Honshu.

Primula suffrutescens A. Gray, Proc. Amer. Acad. Arts 7:371. 1868. (Fig. 1C)—TYPE: USA, California, Sierra Nevada, "trail up Silver Mt.", *Brewer 2047* (holotype, GH; isotype, US!).

Plants efarinose with capitate glands on vegetative parts, glabrous. Stems strongly rhizomatous, not woody, often densely covered with marcescent leaves. Scape to 15 cm high, bearing dense rosettes of leaves at the apex. Leaves including the petiole to 4 cm long, blade somewhat fleshy, 0.5–0.9 (1.1) cm wide, cuneate-spathulate, margins crenate to dentate with 3–8 teeth, tapering gradually to indistinct winged petioles. Involucral bracts lanceolate, plane at the base, densely glandular. Umbels 2–9 flowered; pedicels 0.4–1.2 cm long. Flowers distylous. Calyx green, 0.4–0.8 cm long, urceolate, divided up to $\frac{2}{3}$ the length by lanceolate teeth. Corolla rose-pink, throat yellow, tube 0.6–1.0 cm long, twice the length of the calyx; limb 1.0–2.0 cm wide, lobes emarginate. Stamens ca. 2 mm long, located at the top of the corolla tube in thrum plants and near the middle in pin plants; stigma capitate, located in reciprocal positions to stamens. Capsule globose, ca. 5 mm in diameter, slightly shorter than the calyx. Seeds brown, 1–1.5 mm long, reticulate, angular with flanged edges. Chromosome number: $2n = 44$ (Bruun 1932).

Distribution. Rocky alpine slopes above 3300 meters, in weathered granite soils and rock fissures of the Sierra Nevada and northern mountains of California (Fig. 2B).

Representative specimens. USA, California, Alpine Co., Folger Peak, *Eggleston 9621* (GH); Fresno Co., Mt. Gould, *Sharsmith 3218* (GH); Inyo Co., Kearsarge Pass trail west of Independence, *Alexander and Kellogg 3258* (GH, US); Madera Co., volcanic ridge east of Minaret Lake, *Sharsmith 4539B* (GH); Mono Co., hill above

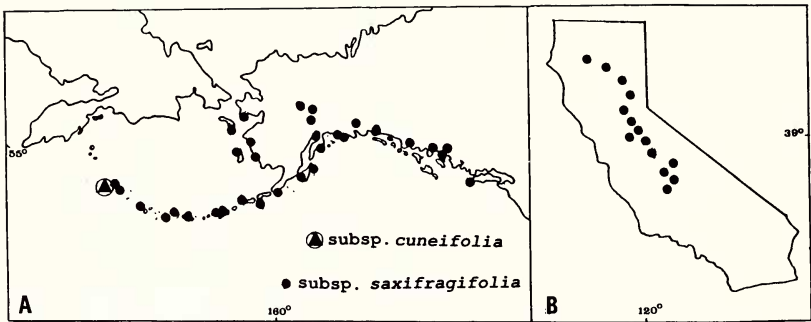


FIG. 2. A. Distribution of *Primula cuneifolia* in North America. B. Distribution of *P. suffrutescens*. Dots indicate more than 1 collection.

Mammoth, *Clausen 70-102* (GH); Nevada Co., above Troy Lake, 25 Jul 1896, *Sonne s.n.* (GH); Placer Co., Ward's Peak, *Sonne 214* (GH); Plumas Co., Luther Ridge between Wade Lake and Spencer Lake, 12 Aug 1969, *Williams s.n.* (G); Siskiyou Co., Caribou Basin near Sawtooth Ridge, *Ferlatte 1045* (K); Trinity Co., 4 miles north of Dedrick, *Hitchcock 5397* (GH); Tulare Co., Sky Blue Lake, *Howell 26007* (GH).

Primula has long been known as an example of distyly (Darwin 1884), a reproductive syndrome where two floral morphs exist with reciprocal placement of androecium and gynoecium. Distylous *Primulas* have a strong intramorph incompatibility system that dictates obligate outcrossing mediated by insect pollen vectors. In comparison, a simple mutation can create a self-compatible homostylous morph with juxtaposed sexual organs (Ganders 1979). Because self-compatibility and the proximity of anthers and stigma facilitate self-fertilization, homostyly is highly adaptive for colonization and may be of selective advantage when pollinator service becomes unreliable (Baker 1966).

The two subspecies of *Primula cuneifolia* described here differ principally in their reproductive biology: subsp. *cuneifolia* is distylous and subsp. *saxifragifolia* is homostylous. I believe they represent an outcrossing progenitor and a self-fertile derivative, respectively. The change in reproductive biology probably occurred during the Pleistocene when climatic perturbations and glacial fluctuations had a severe impact on the insect fauna of the Aleutian-Commander-Kurile island chain (Lindroth 1963), with presumable consequences for pollination. Selection for assured fertilization could thus promote the establishment of a mutant homostylous morph. Subspecies *saxifragifolia* probably originated near the ice margin and spread rapidly as the Aleutian glaciers began to retreat ca. 11,000 years ago (Thorsen and Hamilton 1986). It may not have been able to compete with

the outcrossing populations in the ice-free areas to the south, and consequently migrated only to the east as the ice retreated and left open habitats. Today subsp. *saxifragifolia* is found principally in North America except for a few locations in the Commander Islands and Kamtschatka. In North America subspecies *cuneifolia* inhabits only the western Aleutian Islands, and most of its distribution lies in Kamtschatka. This subspecies, and the additional distylous taxa found in Japan, may be limited to the Asiatic coast by contemporary pollinator and/or climatic restrictions.

The evolutionary position of *Primula suffrutescens* is problematic. As a tetraploid, it is the only polyploid in the section. Like the Asiatic members, it is found on igneous metamorphosed bedrock. Unlike *P. cuneifolia* subsp. *saxifragifolia*, *P. suffrutescens* is distylous and thus not an efficient colonizer. It may represent the only extant member of a more continuous preglacial extension of sect. *Cuneifolia*, surviving glaciation at low elevations on the east slope of the Sierra Nevada.

As well as indicating a biogeographic link between the California mountains and northern Japan, *Primula* sect. *Cuneifolia* also provides a disjunct link to the European Alps. Cytologically, anatomically, and morphologically, this section is most similar to sect. *Auricula* Duby which is limited to mountainous regions of Europe. Section *Auricula* is known for the narrow endemism of its members, their tendency to hybridize in cultivation, and their high levels of polyploidy. It shares with sect. *Cuneifolia* the developmental character of involute veneration, and the morphological characters of toothed leaf margins, globose capsules, deeply divided calyces, capitate glands, and flanged seed margins. Rhizomes and persistent leaf remains similar to those seen in *P. suffrutescens* are common. Section *Auricula* differs from sect. *Cuneifolia* in having more coriaceous leaves, consistently higher chromosome numbers ($4x-11x$) and pollen exine with three separate rather than fused colpi (Spanowsky 1962). Smith and Fletcher (1948) first noted the resemblance of the two sections, and suggested that a common ancestor must have been extirpated in the Asiatic landmass between where the two sections are found today.

In spite of its small size and limited distribution, sect. *Cuneifolia* holds an important position in the genus *Primula*. Biogeographically it links Europe, Asia, and western North America; developmentally it appears to provide a link to other genera in the Primulaceae; and reproductively it provides an example of how an outcrossing breeding system can convert to selfing with taxonomic and biogeographic implications. Section *Cuneifolia* is one of the few well-defined sections in a taxonomically complex genus, and it may well provide important phylogenetic connections both within *Primula* and within the family Primulaceae.

ACKNOWLEDGMENTS

I am grateful to the curators and staff at ALA, BM, CAS, COLO, E, GH, K, and US for assisting my work there and for lending specimens. I also thank the American Society of Plant Taxonomists for the John Ayres Travel Award which made it possible to visit BM, E, and K. Carolyn Parker participated in Alaskan fieldwork, and Kay Holmes did the drawings.

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(Received 23 Apr 1990; revision accepted 12 Oct 1990.)